Taxonomic Relatedness of Spider and Carabid Assemblages in a Wetland Ecosystem

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ABSTRACT

Traditional community indices, i.e. Shannon diversity and Simpson's dominance, are generally used to describe biological assemblages in order to infer ecological trends about the effects of disturbance. Such indices are correlated with species richness and abundance and may be strongly influenced by sampling effort. Conversely, taxonomic relatedness indices show interesting statistical properties and are independent from sampling effort. Additionally, high values of taxonomical relatedness indices have been proved to reflect habitat functionality in marine ecosystems. Their use in terrestrial ecosystems is rare, and despite their good potential, they have never been used for biodiagnostic purposes. In this paper we present the first application of taxonomical relatedness indices to arthropod assemblages (namely spiders and carabids) and their comparison with several traditional community parameters that are generally used for the evaluation of environmental disturbance. The study was set in a wetland area within the Natural Reserve of Fondo Toce (NW-Italy). Four different habitats with different degrees of disturbance (a bed of reeds, a mown meadow, a riparian wood with mesophilous elements and a transitional mesohygrophilic area invaded by non-native vegetation) were sampled using pitfall traps. The spider and carabid assemblages occurring in each habitat were characterized by means of Multidimensional Scaling (MDS) and by several community parameters, including abundance, species richness diversity, taxonomic relatedness indices and some descriptive functional traits. Differences among habitats were tested with Generalized Linear Models. Correlations among community parameters were evaluated with Spearman's rank correlations. According to MDS plots, both assemblages were clearly separated in relation to habitat type. When considering the parameters describing the assemblages in relation to disturbance, the taxonomical approach was found to be particularly suitable for spiders, for which the less disturbed habitat were characterized by higher values of average taxonomical distinctness. Furthermore, functional groups of spiders resulted more evenly distributed in undisturbed habitats. The functional approach was found particularly appropriate for carabids, which responded to disturbance in terms of decrease of biomass (average body size) and increase in the proportional abundance of macropterous individuals.

INTRODUCTION

The potentiality of arthropods as bioindicators has been widely recognized, especially when describing and characterizing different habitats and environmental conditions. The analysis of arthropod communities is traditionally based on the characterization of the assemblages by means of diversity indices, like for example species richness, Shannon diversity and Simpson dominance. Such indices are strongly dependent on sampling effort and in general terms they do not take into account any phylogenetic, taxonomic, or functional variability among the species within a community (Heino et al. 2005). The work by Clarke & Warwick (1995) proposes several new indices based on the taxonomic relations between the species in a community in order to quantify the average degree to which individuals in an assemblage are related to each other. From this point of view, an assemblage comprising a group of closely related species is less diverse than an assemblage of the same number of more distantly related species, for example belonging to different families. Those new indices show several interesting statistical properties, namely the virtual independence from the sampling effort (Clarke & Warwick 1998). Taxonomic diversity (Δ) is the expected path length between any two randomly chosen individuals from the sample. Taxonomic distinctness (Δ^*) is a modification of the former index in order to remove some of the overt dependence of Δ on the species abundance distribution. The average taxonomic distinctness (Δ^+), considers only presence/absence information for each species.

If we assume that taxonomic diversity is closely related to ecological diversity and functionality, it is furthermore evident that the evaluation of this parameter may be crucial to evaluate the structure and the degree of disturbance of a certain ecosystem (Hughes 1994, Tilman 1996). Taxonomic relatedness indices have been suggested to be less sensitive than species richness to intrinsic differences among habitat types, and thereby to be more amenable to detect degradation due to anthropogenic effects (Warwick & Clarke 1995, 1998). Taxonomic relatedness indices have been mostly used in marine and freshwater ecology studies and there are just a few works focusing on terrestrial ecosystem (Banos-Picon et al. 2009, Gresens & Ferrington 2008, von Euler & Svensson 2001). Furthermore, none of them refers about the application of such indices to ground dwelling arthropods and about their use for biodiagnostic purposes.

Ground-dwelling arthropods are small, diverse and sensitive to environmental variability and may be therefore used as indicators of habitat heterogeneity, ecosystem

diversity and environmental stress (McGeoch 1998). Spiders (Arachnida, Araneae) and ground beetles (Coleoptera, Carabidae), in particular, have been widely recommended as bioindicators (Churchill 1997; Rainio and Niemela 2003). The few researches which focused contemporaneously on both groups showed that both are negatively affected by anthropogenic activities (Alaruikka et al. 2002; Öberg & Ekbom 2006; Pearce & Venier 2006, Negro et al. 2009, Negro et al. 2010).

Since the potentiality of spiders as bioindicators were highlighted (Allred 1975, Clausen 1986, Marc et al. 1999), several ecologists used spider assemblages to describe and characterize different habitats and different environmental conditions. Spiders proved to be valuable for the evaluation of anthropic disturbance in several cases (Aakra 2000, Chen & Tso 2004, Sattler et al. 2010, Maelfait et al. 1998, Negro et al. 2010). Their bioindicative potentialities mostly derive from the peculiar features of these arthropods: they are abundant, ubiquitous, they are obliged predators, they exploit different ecological niches and, according to their diversified and multiple hunting strategies, they may reflect the complexity of an ecosystem (Marc et al. 1999). Alterations in microhabitats may influence several aspects of animal communities as the number and diversity of niches, local abundance, and guild compositions (Montaña et al. 2006). Spiders may be particularly suitable for this approach because they can be sorted in "functional groups" (or guilds), according to different hunting strategies. The soundness of this approach was proved in different ecological studies concerning for example forests (Huang et al. 2011), perennial agroecosystems (Isaia et al. 2006) and pasture management (Batary et al. 2008).

Carabids are frequently used to indicate habitat alteration. They have been used in grasslands and boreal forests where species number and/ or abundances have been noted to change along a habitat disturbance gradient (Niemela et al. 2006). They have also been used in many other habitats like for example in agroecosystems (Cole et al. 2002), high altitude areas (Negro et al. 2010, Gobbi et al. 2011) and urban-rural ecosystems (Sadler et al. 2006).

Despite common trends have been found (poorly dispersing specialist species decrease with increased disturbance while small generalist species with good dispersal ability increase (Rushton 1989, Kotze & O' Hara 2003), according to Rainio and Niemela (2003), there is, however, not enough research to determine how suitable carabids are for biodiversity studies, or how well they represent the response of other species. However, Gobbi & Fontaneto (2008) suggested that the analyses of ground

beetle species assemblages commonly performed in applied ecological studies may be potentially misleading: the species richness approach can be too reductive for the characterization of different assemblages occurring in different habitats, especially when focusing on their sensitivity to human disturbance. In response to this, Gobbi & Fontaneto (2008) proposed the taxonomical approach to characterize the carabid assemblages of different habitats with different degree of anthropogenic disturbance. Despite they did not explicitly refer to Clarcke and Warwick's indices (Δ, Δ* and Δ+), they calculated the phylogenetic distances between species using the branching topology of a taxonomic tree. All pairwise species distances within each assemblage were computed using their topological distances (number of segments separating two species in the taxonomic dendrogram, with nodes identified by the taxonomic categories from species to family). Anyway, such approach did not reveal any significant effect of habitat typology on carabid assemblages. On the other hand, in order to better characterize the assemblages of different habitats with different degrees of disturbance, several authors (Ribera et al. 2001, Purtauf et al. 2005, Gobbi & Fontaneto 2008), analysed ecological and functional traits of carabid assemblages like wing morphology (macropterous, full-sized wings; brachypterous, reduced wings or wingless), diet, body size and trophic rank. The functional approach proved to be more effective that the taxonomical one, underlying significant differences in habitats with different degree of disturbances with minor presence of brachypterous, large and predator species in more disturbed habitats (Gobbi & Fontaneto 2008). Species richness of carnivores also proved to be very sensitive to landscape simplification (Purtauf et al. 2005).

In view of future applications of the taxonomical approach, the aim of our study is to test taxonomical relatedness indices on spider and carabid assemblages in order to characterize different habitats with different degrees of environmental disturbance in a wetland ecosystem. The response of taxonomical relatedness indices to disturbance is also compared with the one given by the traditional community indices (such as species richness, abundance, Shannon's diversity and Simpson's dominance) and the one given by functional traits parameters (biomass expressed as average body size of the individuals of each assemblage, evenness of functional groups for spiders and wing morphology for carabids), in order to highlight the potential of taxonomical relatedness in terms of biodiagnostic use.

MATERIALS AND METHODS

Study area

The study was carried out in the Natural Special Reserve of Fondo Toce located on the shore of the Lake Maggiore (Verbania, NW-Italy). The Reserve includes the mouth of the Toce River and the alluvial plain of Fondo Toce. Several habitats are included in the protected area: a large bed of reeds (BR), a contiguous transitional mesohygrophilic area invaded by non-native vegetation (MV), a riparian wood with mesophilous elements (RW) and a mown meadow (MM). The Reserve is remarkably threatened by the intense human activities around it, including urbanization, tourism and infrastructures such as highways and national roads. Furthermore, a big popular campsite is located at the border of the Reserve. The bed of reeds (adjacent to the latter) covers an area of 28 hectares and is dominated by *Phragmites australis*. This habitat represents the most endangered habitat in the area and its conservation represents the main aim for which the Reserve was established in 1990. The riparian wood with mesophilous elements is dominated by *Salix alba*, *Alnus glutinosa* with scattered *Quercus* sp. and *Tilia* sp. The transitional mesohygrophilic area (1.3 hectares) is infested by goldenrod *Solidago canadensis*, a non-native species introduced in Europe from North America. The invasion of this species was first reported from Europe in 1645 and in China around 1930. Today it is widespread and invasive all over Europe and increasingly in East Asia. Given its broad tolerance to nutrients and humidity it colonizes a variety of different habitats, including natural habitats as well as derelict land, road sides and dry floodplains. At several locations *Solidago canadensis* is considered a threat to biodiversity (Global Invasive Species Database 2005).

The four habitats within the Reserve are characterized by different degrees and typologies of disturbance: the mown meadow is mowed twice a year during spring and summer; the transitional mesohygrophilic area is invaded by non-native vegetation replacing the natural vegetal association of *Molinietum*; the bed of reed is characterized by natural disturbance related to the seasonal variation of the water level. Despite exceptional events of floods (average recurrence interval 5 to 10 years), the riparian wood with mesophilous elements is characterized by the general absence of both anthropogenic and natural disturbance.

Experimental design

We selected 40 sampling plots in the four different habitats within the Reserve. Ten pitfall traps were placed in each of the four habitats and emptied once a month for four times, from May to September 2009 (112 days of activity, 4 habitats x 10 traps x 4 replicates: 160 traps positioned in all).

Traps were filled with ethylene glycol 50% to kill and preserve specimens. All specimens were stored in vials with 70% ethanol and examined under a stereomicroscope up to 40x. Spiders and carabids were identified whenever possible at species level. Voucher specimens of spiders are stored at the Dipartimento di Biologia Animale e dell'Uomo of Turin University. Voucher specimens of carabids are stored in the Giachino's collection, Turin. Nomenclature of spiders follows Platnick (2011) and nomenclature of carabids follows Fauna Europaea (2011).

Data analysis

Spider and carabid assemblages

An abundance-based richness estimator (ACE) was used to predict expected species richness at the four habitats. Completeness was measured for each site as the percentage of the total number of species predicted by the estimator that we actually observed. The richness estimator was computed using EstimateS 8.0.0 (Colwell 2006). MDS plots (Bray-Curtis distance, 100 random starts) were used to compare spider and carabid assemblages. MDS plots were run with PRIMER-E ver. 6 software package (Clarke & Gorley 2006).

Comparisons among habitats

In all analyses comparing arthropod assemblages occurring in each habitat, we considered the mean value of the 4 replicates as the basic sample unit. In total 40 basic sample units were used. For each basic sample unit we computed species richness (S), abundance (N), Shannon diversity (natural logarithmic form, H'), Simpson diversity (1-lambda' form, 1-λ') and Pielou's evenness (natural logarithmic form, J'). Three taxonomic relatedness indices including taxonomic diversity (Δ), taxonomic distinctness (Δ*) and average taxonomic distinctness (Δ+) were also calculated using the equations reported in Clarcke & Warwick (1998). The taxonomic matrix used for the calculation of taxonomic relatedness indices for spiders (Order Araneae) included three primary ranks: Family, Genus and Species. In order to have

the same number of ranks (3) for the two assemblages, for carabids (Family Carabidae), we added the secondary rank of Subfamily, considering that only the two primary ranks of Genus and Species were available

PRIMER-E, ver. 6 software package (Clarke & Gorley 2006) was used for the calculation of all indices.

Some functional traits characterizing the assemblages (values for single basic sample unit) were also considered: for spiders we computed the evenness of functional groups (assigned referring to Cardoso et al. 2011, FG) and an estimation of the biomass of the assemblage (average body length from clypeus to spinnerets in mm weighted on abundance, AVG; data gathered from literature). In accordance with Gobbi & Fontaneto (2008) for carabid assemblages we computed wing morphology ratio (number of macropterous specimens on total specimens, MACR) and an estimation of the biomass of the assemblage (average body length from clypeus to posterior margin of the elytra in mm weighted on abundance, AVG; data gathered from literature, Casale et al. 2005, Jeannel 1942).

Given that parametric tests could not be properly employed because several assumptions were not met (homoscedasticity was violated and error terms were not always normally distributed), generalized linear models (GLZ) were used to test differences between habitats. Link functions were selected according to McIntyre & Lavorel (1994). Tests for the significance of the effects in the models were performed by means of Wald statistics (Dobson 1990). In the parameter estimation analysis, we used riparian wood with mesophilous elements (RW) as the reference category.

Distribution fitting of indices was performed with Easyfit ver. 5.5. Generalized linear models were calculated using the STATISTICA 6.0 package (StatSoft Italia 2001).

Species richness and abundance of both assemblages and were better described by the Poisson distribution therefore these distributions of errors were assumed and the community parameters were related to explanatory variables via a logarithmic link function. Taxonomic relatedness indices (Δ, Δ^* and $\Delta+$), biomass of both assemblages, Shannon and Simpson diversity of spider assemblages were better described by the Gamma distribution and they were related to explanatory variables via an inverse link function. All other indices (Pielou's evenness for both assemblages, Shannon and Simpson's diversity for carabids), evenness of functional groups of spiders and macropterous ratio of carabids were better described by the

normal distribution and were related to explanatory variables via an identity link function.

Correlation among indices

We used nonparametric Spearman rank-order correlation tests for the analysis of the relationship between indices, referred to both assemblages. Spearman correlations were calculated with STATISTICA 6.0 software package (StatSoft Italia srl 2001). A level of significance of alpha = 0.05 was used for the analysis.

RESULTS

Spider and carabid assemblages

A total of 559 spiders and 1480 carabids were collected. Spiders were belonging to 10 families and 35 species, while for carabids 32 species were identified (9 subfamilies). Lycosidae was the most abundant spider family, followed by Thomisidae, Tetragnathidae and Linyphiidae. The most abundant species were *Pardosa prativaga*, *Trochosa ruricola* and *Ozyptila praticola*. According to Cardoso et al. (2011) we identify 5 different functional groups in our dataset: ground hunters, ambush hunters, orb web weavers, sheet web weavers and other hunters. Most of the spiders belong to ground hunters (69.6 %), followed by ambush hunters (10.8%).

The most abundant carabid species was *Amara aenea* followed by *Harpalus luteicornis*. Most of individuals (77.7%) were macropterous (for the complete list of spiders and carabids species see Appendix 1 and Appendix 2).

Sampling of spiders was adequate for three habitats (riparian wood with mesophilous elements, mown meadow and bed of reeds) given that the most of expected species were effectively caught. For carabids all habitats were sampled adequately. Given this result, for spider assemblages we consider only riparian wood with mesophilous elements (RW), mown meadow (MM) and bed of reeds (BR), while for carabids all habitats were considered in the analysis (Table 1).

MDS plots (fig. 1 and fig. 2) reveal that both spider and carabids assemblages characterize well the four different habitats (stress for Araneae=0.088; stress for Carabidae=0.01).

Comparisons among habitats

GLZ estimates of spider indices (Tab. 2) show that mean values of Shannon diversity are significantly lower in the mown meadow (MM) in respect to the reference category (RW, riparian wood with mesophilous elements, $p<0.05$), while Pielou's evenness and Simpson diversity are significantly higher. All taxonomic relatedness indices (Δ, Δ^* and $\Delta+$) show the same trend: the mown meadow (MM) has significantly lower values ($p<0.05$) while the bed of reeds (BR) shows significantly higher values than the riparian wood with mesophilous elements (RW, $p<0.01$). No significant differences between the reference category and other habitats were found in respect to biomass of spiders while a significant lower evenness of functional groups was observed for the mown meadow (MM, $p<0.05$).

GLZ estimates for carabid assemblages (Tab. 3) show that, compared with the reference category (RW), species richness is significantly higher in the transitional mesohygrophilic vegetation (MV, $p<0.05$) and significantly lower in the bed of reeds (BR, $p<0.01$). No significant differences occur between riparian wood with mesophilous elements (RW) and mown meadow (MM) in terms of species richness. Abundance shows the same trends as species richness, but in this case the mown meadow (MM) has a significantly lower value than the riparian wood with mesophilous elements (RW, $p<0.01$), too. Pielou's evenness is significantly higher in the mown meadow (MM) and in the bed of reeds (BR, respectively $p<0.05$ and $p<0.01$). Shannon diversity index do not show any difference among habitats, while for Simpson diversity index, higher values are found in the mown meadow (MM, $p<0.05$). No significant differences among habitats were found for carabids in respect to taxonomic relatedness indices (Δ in, Δ^* and $\Delta+$).

The biomass of carabids is significantly lower in the mown meadow (MM, $p<0.01$) and significantly higher in the bed of reeds (BR, $p<0.01$) in respect to the reference category (RW). In addition, the macropterous ratio in the reference category (RW), is always lower in respect to all other habitats ($p<0.01$).

Correlations among indices

Results of nonparametric Spearman rank-order correlation show similar results for spider and carabid assemblages (Tab. 4 and Tab. 5). Pielou's evenness (J') and Shannon diversity (H') show significant correlations (negative for J' and positive for H') with species richness (S) and abundance (N) for both assemblages, proving the dependence of these indices from the sampling effort. A similar trend is also found for Simpson's diversity (1-λ') of spiders, showing a positive correlation with S. Taxonomic relatedness indices (Δ, Δ^* and $\Delta+$) show no correlations with S and N, but proved to be correlated with each other. Regarding spider assemblages, Δ and Δ^* are correlated with H' and 1-lambda' and Δ is also correlated with J'. In carabid assemblages Δ is correlated with J', H' and 1-lambda'.

DISCUSSION

Understanding patterns in biological diversity and their underlying causes using diversity indices is one of the most important challenge in ecological studies (Begon et al. 1996). As community indices are abstraction that may be useful when making comparisons among different habitats (Begon et al. 1996), we used both the traditional approach of community indices and the less conventional one of taxonomical relatedness in order to assess the response of carabid and spider assemblages to different degrees and typologies of habitat disturbance. In accordance with literature, we also used the functional approach that proved to be useful for characterization of arthropod assemblages (in particular for carabids) in terms of evaluation of disturbance (Ribera et al. 2001, Purtauf et al. 2005, Gobbi & Fontaneto 2008).

The suitability of carabids and spider assemblages for the characterization of the different habitats is firstly observed by MDS plots (fig. 1 and 2), indicating that spider and carabid assemblages are well differentiated in the four habitats and confirming the strong relation of spiders and carabids to their habitat (Marc et al. 1999, Entling et al. 2007, Schirmel & Buchholz 2011).

The habitat comparisons provide some interesting results in terms of evaluation of environmental disturbance. The most "undisturbed" habitat (riparian wood with mesophilous elements, RW) is characterized for both assemblages by lower values of Pielou's evenness and Simpson diversity when compared to the most disturbed habitat (mown meadow, MM). Furthermore, spider assemblages show higher values of Shannon diversity in the disturbed habitat (mown meadow, MM). These result is in accordance with the Intermediate Disturbance Hypothesis (Sasaki et al. 2009, Svensson et al. 2009), assuming that intermediate levels of disturbance are associated with higher diversity values. The transitional mesohygrophilic area infested by non-native goldenrods (MV) and the mown meadow (MM) may be regarded as example of intermediate disturbance: the first represents a perturbation of the natural evolution of the bed of reeds but (massive colonization of non-native plants) and the latter being characterized by constant physical disturbance derived by human activity. Whether mowing proved to be efficient to maintain plant diversity (Buttler 1992, Cowie et al. 1992, Güsewell et al. 1998), the effect on ground dwelling arthropods is less understood and may be different according to different groups. Concerning spiders,

for example, it has been proved that the less mobile species and the one living in the litter, including rare species, are negatively influenced by mowing (Cattin et al. 2003) while for carabids significant effects were proved according to mowing techniques (Humbert et al. 2008). In addition Schirmel (2010) reports that mowing in heathlands preserve, carabid assemblages that find suitable habitat conditions shortly after management.

In respect to carabid assemblages, significantly higher values of S and N were found in the goldenrod invaded habitat (MV) while, conversely, the mown meadow (MM) show significantly lower values of abundance. The interpretation of these result is unclear, in accordance to the fact that the community is largely dominated by macropterous carabids, with contrasting ecological requirements (Negro et al. 2010). Furthermore, in accordance with Gobbi & Fontaneto (2008), species richness is too reductive for the interpretation of sensitivity of carabid assemblages to human disturbance.

On the other hand, the functional approach proved to be effective for carabids, with higher ratio of macropterous carabids in disturbed habitats, like the mown meadow (MM). Similar conclusions are reported by Gobbi & Fontaneto (2008). In relation to the high dispersal power and high potential in colonizing disturbed habitats (Ribera et al. 2001), winged carabids result more abundant in the disturbed habitats. In accordance with Gobbi & Fontaneto (2008), a minor biomass was found in the most disturbed habitat (mown meadow, MM). Considering that big species are generally linked to stable environments, the higher biomass in the bed of reeds (BR) may suggest that this habitat is more stable in respect to reference category (RW). This result could be biased due to the fact that we used average body size weighted on individuals rather than species, but on the other hand the higher average body size found in this habitat may reflect the absence of anthropogenic disturbance

Biomass of spiders shows no significant differences among habitats. As far as we are concerned, the biomass of spiders is rarely applied in ecological studies evaluating the impact of disturbance. On the other hand, the use of functional groups of spiders gave, in some cases, interesting results. Huang et al. (2011) found that spider guilds respond differently to forest management practices; Isaia et al. (2006) report an increase in the ratio of sheet web weavers in intensive vineyards located in homogeneous agricultural landscapes. In our case, a decrease of the evenness of functional groups per basic sampling unit is observed for disturbed habitats, namely

the mown meadow (MM), attesting the reliability of the use of functional groups of spiders for biodiagnostic purposes.

The indices of taxonomical relatedness of an assemblage could reflect the functionality of the habitat (Warwick & Clarke 1998). In our case the most undisturbed habitats, like the riparian wood with mesophilous elements (RW) and the bed of reeds (BR) are characterized by highly taxonomically diverse spider assemblages. These results are in accordance with Gallardo et al. (2011), suggesting that lower values of taxonomic distinctness and average taxonomic distinctness are associated with higher disturbance. Furthermore, their low value may reflect the absence of a variety of ecological niches that may support complex biological assemblages. Compared to spiders, carabid assemblages seem to be less suitable for the evaluation of environmental disturbance through the application of taxonomical relatedness indices.

As pointed out by Clarke & Warwick (1998), one of the most interesting features of the taxonomical approach is the independence from sampling effort. The study of correlations among indices confirms this property: taxonomic diversity, taxonomic distinctness and average taxonomic distinctness (Δ, Δ^* and $\Delta+$) for both assemblages are not correlated with abundance (N) that reflects the sampling effort. Additionally, $\Delta+$ shows no correlations with any traditional community indices, suggesting the provision of a different kind of information for the characterization of the assemblage. This observation is in accordance with the study of Gallardo et al. (2011), in which it was found that while Shannon diversity (H') increase, both variation in taxonomic distinctness and average taxonomic distinctness (Δ^* and $\Delta+$) scores remain low.

In view of their taxonomical hierarchy (Order level), the relative stability of their systematic, their sensitivity to habitat disturbance and, most of all, their huge ecological diversification (for example in terms of hunting strategies and belonging to different guilds, see Cardoso et al. 2011), the taxonomical approach applied to spider assemblages, seems to provide a suitable way to characterize habitat disturbance. In addition, the independence from sampling effort may provide reliable results when dealing with small datasets ore presence/absence data. In particular, in view of future studies, the average taxonomical distinctness ($\Delta+$) of spider assemblages seems to provide an effective measure for biodiagnostic purposes: it is not correlated with any

of the other traditional community indices and detects significant differences among habitats with different degrees of disturbance.

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Figure legends

Figure 1. Two dimensional MDS plot for spider assemblages (stress= 0.088). Each point describes a single basic sample unit. RW= riparian wood with mesophilous elements; BR= bed of reeds; MV= transitional mesohygrophilic area; MM= mown meadow.

Figure 2. Two dimensional MDS plot for carabid assemblages (stress= 0.01). Each point describes a single basic sample unit. RW= riparian wood with mesophilous elements; BR= bed of reeds; MV= transitional mesohygrophilic area; MM= mown meadow.

Table legends

Table 1. Results of the abundance-based richness estimator (ACE) for Araneae and Carabidae for each habitat. RW= riparian wood with mesophilous elements; BR= bed of reeds; MV= transitional mesohygrophilic area; MM= mown meadow

Table 2. GLZ results for spider assemblages. Riparian wood (RW) is the reference category (BR=bed of reeds; MM=mown meadow). Distribution models and link functions are indicated in brackets (* $p<0.05$; ** $p<0.01$).

Table 3. GLZ results for carabid assemblages. Riparian wood (RW) is the reference category (BR=bed of reeds; MV=mesohygrophilic vegetation area; MM=mown meadow). Distribution models and link functions are indicated in brackets (* $p<0.05$; ** $p<0.01$).

Table 4. Correlations for spider assemblages. The asterisk indicates correlation ($p<0.05$). RW= riparian wood with mesophilous elements; BR= bed of reeds; MV= transitional mesohygrophilic area; MM= mown meadow. S= species richness; N= abundance; H'= Shannon diversity (natural logarithmic form); 1-λ'= Simpson diversity; J'= Pielou's evenness (natural logarithmic form). Δ= taxonomic diversity; Δ*= taxonomic distinctness; Δ+= average taxonomic distinctness.

Table 5. Correlations for carabid assemblages. The asterisk indicates correlation ($p<0.05$). RW= riparian wood with mesophilous elements; BR= bed of reeds; MV= transitional mesohygrophilic area; MM= mown meadow. S= species richness; N= abundance; H'= Shannon diversity (natural logarithmic form); 1-λ'= Simpson diversity; J'= Pielou's evenness (natural logarithmic form). Δ= taxonomic diversity; Δ*= taxonomic distinctness; Δ+= average taxonomic distinctness.

Appendix legends

Appendix 1. Spider species listed in systematic order (nomenclature follows Platnick 2011) and abundance (N).

Appendix 2. Carabid species in systematic order (nomenclature follows Fauna Europaea ver. 2.4, 2011) and abundance (N).

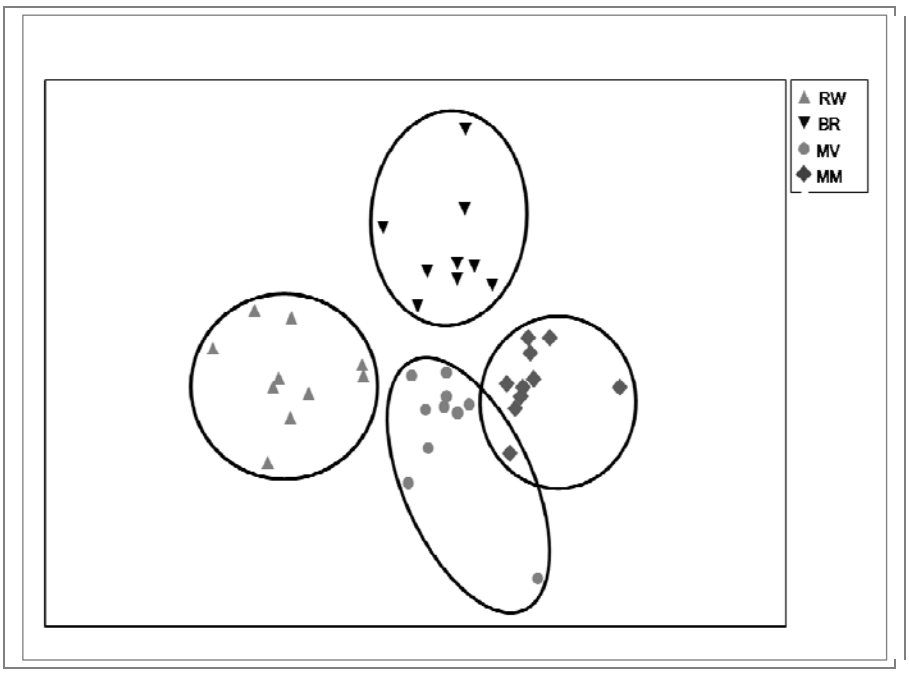

Figure 1.

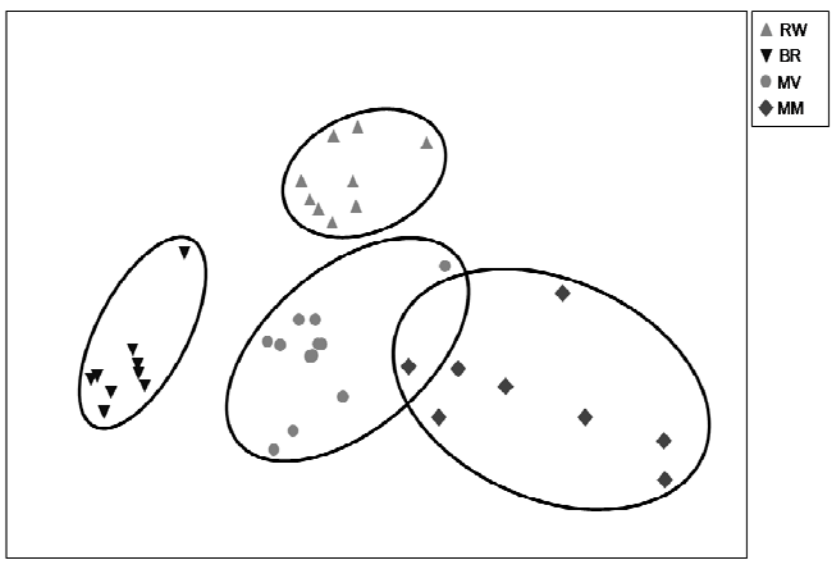

Figure 2.

21**Table 1.**

Taxa	Habitat	Observed species	ACE	% of estimate species
Araneae	RW	10	10.799	92.6
	BR	9	9.802	91.8
	MV	12	30.487	39.4
	MM	17	21.487	79.1
Carabidae	RW	19	19.937	95.3
	BR	7	7.831	89.4
	MV	18	19.457	92.5
	MM	16	20.486	78.1

22
23**Table 2.**

	Habitat	Estimate	Standard - Error	Wald - Stat.	p
S	BR	-0.047	0.130	0.903	0.499
(Poisson, Log link)	MM	0.202	0.122	27284	0.099
N	BR	-0.237	0.076	9617	0.001**
(Poisson, Log link)	MM	0.084	0.070	1440	0.230
J'	BR	-0.006	0.030	0.040	0.841
(Normal, Identity link)	MM	0.055	0.027	408235	0.043*
H'	BR	-0.072	0.123	0.339	0.560
(Gamma, Inverse link)	MM	0.221	0.108	421883	0.039*
1-Lambda'	BR	-0.066	0.057	1361	0.243
(Gamma, Inverse link)	MM	-0.121	0.053	5291	0.021*
Δ	BR	-0.003	0.001	72658	0.007**
(Gamma, Inverse link)	MM	0.002	0.001	38165	0.051
Δ*	BR	-0.001	0.000	12890	0.000**
(Gamma, Inverse link)	MM	0.003	0.000	57490	0.000**
Δ+	BR	-0.001	0.000	14377	0.000**
(Gamma, Inverse link)	MM	0.003	0.000	48208	0.000**
AVG	BR	-0.355	0.395	0.811	0.368
(Gamma, Inverse link)	MM	0.504	0.395	1.630	0.202
J'FG	BR	0.277	0.146	3.605	0.057
(Normal, Identity link)	MM	-0.501	0.239	4.417	0.035*

Table 3.

	Habitat	Estimate	Standard - Error	Wald - Stat.	p
S (Poisson, Log link)	BR	-0.433	0.146	87519	0.003**
	MV	0.236	0.109	47120	0.029*
	MM	-0.216	0.140	23901	0.122
N (Poisson, Log link)	BR	-0.642	0.074	74239	0.000**
	MV	0.224	0.052	18238	0.000**
	MM	-0.709	0.079	80050	0.000**
J' (Normal, Identity link)	BR	0.093	0.035	6699176	0.008**
	MV	-0.003	0.036	0.007	0.931
	MM	0.080	0.040	396536	0.046*
H' (Normal, Identity link)	BR	-0.079	0.173	0.208	0.648
	MV	0.137	0.135	101932	0.313
	MM	-0.144	0.175	0.671	0.413
1-Lambda' (Normal, Identity link)	BR	-0.065	0.100	0.420	0.5170
	MV	0.022	0.092	0.060	0.806
	MM	0.193	0.098	391422	0.047*
Δ (Gamma, Inverse link)	BR	-0.001	0.001	0.238	0.626
	MV	-0.001	0.001	1,213	0.271
	MM	0.001	0.001	0.329	0.566
Δ* (Gamma, Inverse link)	BR	0.001	0.001	1,106	0.293
	MV	0.000	0.001	0.029	0.864
	MM	0.000	0.001	0.249	0.618
Δ+ (Gamma, Inverse link)	BR	0.001	0.001	1,181	0.277
	MV	0.000	0.001	0.290	0.590
	MM	0.001	0.001	0.469	0.493
AVG (Gamma, Inverse link)	BR	-0.041	0.002	271.794	0.000**
	MV	-0.005	0.003	2.749	0.097
	MM	0.024	0.004	37.644	0.000**
MACR (Normal, Identity link)	BR	0.408	0.059	48.364	0.000**
	MV	0.311	0.060	26.927	0.000**
	MM	0.416	0.060	48.051	0.000**

43**Table 4.**
44

	S	N	J'	H'(loge)	1-λ'	Δ	Δ*	Δ+
S								
N	0.741*							
J'	-0.361*	-0.538*						
H'(loge)	0.922*	0.585*	-0.085					
1-λ'	0.574*	0.155	0.440*	0.807*				
Δ	0.312	0.011	0.346*	0.487*	0.674*			
Δ*	-0.271	-0.175	-0.096	-0.332*	-0.353*	0.445*		
Δ+	-0.148	-0.054	-0.154	-0.222	-0.308	0.460*	0.957*	

45**Table 5.**
46

	S	N	J'	H'(loge)	1-λ'	Δ	Δ*	Δ+
S								
N	0.825*							
J'	-0.592*	-0.683*						
H'(loge)	0.808*	0.443*	-0.142					
1-λ'	0.024	-0.182	0.634*	0.388*				
Δ	0.147	-0.091	0.490*	0.508*	0.846*			
Δ*	0.228	0.174	-0.281	0.205	-0.290	0.262		
Δ+	0.091	0.016	-0.079	0.174	-0.181	0.333*	0.938*	

47**Appendix 1.**
48

FAMILY/Species	RW	BR	MV	MM
THERIDIIDAE				
Euryopis flavomaculata (C.L.Koch, 1836)	7	0	0	0
Robertus lividus (Blackwall, 1836)	1	0	0	0
LINYPHIIDAE				
Bathyphantes gracilis (Blackwall, 1841)	0	10	0	0
Ceratinella brevis (Wider, 1834)	0	0	3	1
Diplostyla concolor (Wider, 1834)	1	0	0	0
Erigone dentipalpis (Wider, 1834)	0	0	0	2
Gnathonarium dentatum (Wider, 1834)	0	13	0	1
Gongylidiellum murcidum Simon, 1884	0	1	0	0
Nematogmus sanguinolentus (Walckenaer, 1842)	0	2	0	0
Oedothorax retusus (Westring, 1851)	0	0	0	2
Walckenaeria antica (Wider, 1834)	0	0	1	0
TETRAGNATHIDAE				
Pachygnatha clercki Sundevall, 1823	0	8	0	0
Pachygnatha terilis Thaler, 1991	5	0	35	0
Tetragnatha nigrita Lendl, 1886	0	0	2	0
ARANEIDAE				
Argiope bruennichi Scopoli, 1772	0	0	0	1
LYCOSIDAE				
Arctosa leopardus (Sundevall, 1833)	0	2	1	19
Pardosa alacris (C. L. Koch, 1833)	10	0	0	0
Pardosa cribrata Simon, 1876	0	0	0	3
Pardosa prativaga (L.Koch, 1870)	0	2	62	14
Pardosa proxima (C.L.Koch, 1847)	0	0	0	40
Pardosa torrentum Simon, 1876	0	0	1	6
Pirata hygrophilus Thorell, 1872	9	0	0	0
Pirata piraticus (Clerck, 1757)	0	37	1	0

Trochosa hispanica Simon, 1870	55	0	0	0
Trochosa ruricola (De Geer 1778)	6	17	42	38
Xerolycosa miniata (C.L.Koch, 1834)	0	0	0	6
HAHNIIDAE				
Antistea elegans (Blackwall, 1841)	0	13	1	0
LIOCRANIDAE				
Liocranoeca striata (Kulczyński, 1882)	10	0	1	0
CORINNIDAE				
Phrurolitus festivus (C.L. Koch, 1835)	0	0	0	3
GNAPHOSIDAE				
Drassyllus pusillus (C. L. Koch, 1833)	0	1	0	0
Micaria pulicaria (Sundevall, 1831)	0	0	0	1
THOMISIDAE				
Ozyptila praticola (C. L. Koch, 1837)	48	0	0	0
Ozyptila trux (Blackwall, 1846)	0	0	0	2
Ozyptila simplex (O.P.-Cambridge, 1862)	0	0	9	1
SALTICIDAE				
Myrmarachne formicaria (De Geer, 1778)	0	0	0	2

Appendix 2.

SUBFAMILY / Species	RW	BR	MV	MM
CARABINAE				
Carabus granulatus interstitialis Duftschmid, 1812	88	0	51	3
NEBRINAE				
Nebria (Boreonebria) rufescens (Stroem, 1768)	17	0	0	0
ELAPHRINAE				
Elaphrus (Elaphroterus) aureus P. Muller, 1821	2	0	0	1
TRECHINAE				
Asaphidion flavipes (Linnaeus, 1761)	3	0	0	7
Metallina (Metallina) properans (Stephens, 1828)	1	0	0	0
PTEROSTICHINAE				
Poecilus versicolor (Sturm, 1824)	9	8	95	3
Pterostichus (Argutor) vernalis Panzer, 1796	5	1	2	0
Pterostichus (Phonias) strenuus (Panzer, 1796)	107	2	6	2
Pterostichus (Platysma) niger (Schaller, 1783)	9	0	6	0
Pterostichus (Morphnosoma) melanarius (Illiger, 1798)	2	0	4	0
Pterostichus (Pseudomaseus) nigrita (Paykull, 1790)	15	0	0	0
Pterostichus (Pterostichus) pedemontanus Ganglbauer, 1891	1	0	6	0
Abax continuus Baudi, 1876	52	0	76	8
Amara (Amara) aenea (De Geer, 1774)	253	0	12	1
Amara (Amara) familiaris (Duftschmid, 1812)	0	0	10	6
CHLAENIINAE				
Chlaeniellus nitudulus (Schrank, 1781)	0	2	10	6
OODINAE				
Oodes helopioides (Fabricius, 1792)	3	19	19	2
HARPALINAE				
Anisodactylus binotatus (Fabricius, 1787)	1	0	36	0
Anisodactylus nemorivagus (Duftschmid, 1812)	2	0	2	0
Diachromus germanus (Linnaeus, 1758)	0	0	0	2
Stenolophus teutonus (Schrank, 1781)	3	0	20	10
Ophonus (Pseudophonus) rufipes (Degeer, 1774)	0	0	1	2
Harpalus (Harpalus) luteicornis (Duftschmid, 1812)	213	0	2	0
PLATYNINAE				
Calathus fuscipes graecus Dejean, 1831	0	33	0	0
Agonum (Agonum) muelleri (Herbst, 1784)	5	45	2	0
Agonum (Melanagonum) lugens (Duftschmid, 1812)	0	7	0	48
Agonum (Punctagonum) sexpunctatum (Linnaeus, 1758)	37	3	1	0
Agonum (Europhilus) thoreyi Dejean, 1828	1	0	0	0
Limodromus assimilis (Paykull, 1790)	66	0	2	1